13

Myriapods and Arthropleurids

Joseph T. Hannibal

Millipedes, known also as "centipedes" or "multipedes," are insects belonging to the earthworm genus, hairy, with numerous feet, forming curves as they crawl, and contracting themselves when touched: the Greeks give to this insect the name of "oniscos," others, again, that of "tylos" ["iulos"].[1] Boiled with leek-juice in a pomegranate rind, it is highly efficacious, they say, for pains in the ears. *The Natural History of Pliny.*

Myriapods (many-legged animals) are secretive arthropods typically associated with the forest floor. They possess a head with a single pair of antennae, many basically similar trunk segments, and nine or more pairs of legs. Their body segments may be divided into distinct dorsal (top), lateral (side), and ventral (bottom) parts known as tergites, pleurites, and sternites. The tergites, pleurites, and sternites may be partially or completely fused.

There are four extant classes of myriapods: the Diplopoda (millipedes or "thousand-leggers"), Chilopoda (centipedes or "hundred-leggers"), Symphyla (symphylids), and Pauropoda (pauropods), the first three of which have also been found as fossils. The evolutionary relationships between these classes is at present uncertain. There is at least one similar, extinct class of arthropods, the Arthropleuridea (arthropleurids).

Classification of fossil myriapods and allied forms at the species level is based on external characters such as the number of segments, ornamentation, and arrangement of spines, but that of extant forms is typically based on characters of the male genitalia. The characteristics of the main groups include:

Diplopoda (millipedes). Medium-sized, primarily herbivorous myriapods, up to about 300 mm (12 in.) in length. The trunk segments of these slow-moving arthropods are composed of two partially coalesced segments, one anterior and the other posterior. Millipedes thus have two pairs of legs per trunk segment (Silurian–Recent).

Chilopoda (centipedes). Medium-sized myriapods, up to 380 mm (15 in.) in length. These are fast-moving, carnivorous forms with generally one pair of legs per trunk segment (Silurian–Recent).

Symphyla. Very small myriapods, 2–8 mm (0.1–0.3 in.) in length, with 15 to 22 trunk segments and 12 pairs of legs (Oligocene–Recent).

Pauropoda. Minute myriapods, usually less than 2 mm (0.1 in.) long, with 9 to 11 trunk segments, which each bear a pair of legs, and a tail segment (Recent; the lack of fossil forms is probably due to their small size).

Arthropleuridea. Minute to gigantic myriapod-like arthropods, up to about 2 m (6.6

1. This account, like other Greco-Roman references, appears to confuse true myriapods, which are many-legged arthropods, with caterpillars, which are insects, and other animals. Such confusion continues to some extent among the general populace today. Greek names such as *iulos* and *oniscos* are now parts of the names of various myriapods.

ft.) in length, with about 30 body segments and two pairs of legs per body segment, at least on some segments. Probably herbivorous. These forms share several major characteristics (multiple body segments, many pairs of legs, etc.) with millipedes and centipedes, but their exact relationship with them is problematical (Silurian–Pennsylvanian).

Fossil Myriapods

A multilegged marine animal that at least superficially resembles a myriapod has been reported from the Cambrian (Robinson, 1990), but this form may instead be a polychaete annelid (W. Shear, personal communication, 1992). Possible, but not likely, millipede burrows have been reported from the Ordovician (Retallack and Feakes, 1987). The first body fossils of definite millipedes are Late Silurian in age (Almond, 1985), as are possible centipedes (Jeram et al., 1990). Arthropleurids are first found in Upper Silurian rocks. Early occurrences of myriapods in the fossil record are reviewed by Gray and Shear (1992) and the ecology of Paleozoic myriapods is reviewed by Shear and Kukalova-Peck (1990).

The first diverse assemblages of myriapods and arthropleurids to appear in the fossil record are those found in the Carboniferous rocks of North America and Europe. A large number of species have been described from these strata, especially from the Mazon Creek deposits and the "gas coal" of Nýřany, Czech Republic. More species of fossil myriapods, including both millipedes and centipedes, have been described from the Mazon Creek deposits than from any other locality in North America. Arthropleurids are also known from these deposits.

Initial descriptions and interpretations of Mazon Creek myriapods were made by famed paleontologists Fielding Bradford Meek and Amos Henry Worthen and the esteemed entomologist and paleontologist Samuel H. Scudder. Their pioneering work (including Meek and Worthen, 1868; Scudder, 1882, 1890) was of great importance. Until recently, most of our knowledge of Carboniferous myriapods was based on the work of Scudder and of Anton Fritsch, who studied myriapods found in the "gas coal" as well as some forms found at Mazon Creek (Fritsch, 1907). The early work of Scudder and others, however, is often lacking in detail and accuracy; the back ends of some forms were even described as the front ends! More than 20 species at one time referred to as myriapods have been described from the Mazon Creek deposits, but not all of these species are valid. Also, there has been debate over whether some of these were in fact myriapods. Recently, *Ilyodes* Scudder, 1890, and *Palaeocampa* Meek and Worthen, 1868, once thought to be myriapods, were found to belong to other groups. *Ilyodes* is now known to be an onychophoran and *Palaeocampa* a polychaete worm (Rolfe et al., 1982). See Chapter 7A for a discussion of *Palaeocampa*, and Chapter 15C for *Ilyodes*.

The classification and systematics of species found at Mazon Creek, as well as fossil myriapods in general, are badly in need of revision. The latest comprehensive review of fossil myriapods in general is that of Hoffman (1969), although Silurian and Devonian forms have been reviewed by Almond (1985).

The millipedes, centipedes, and arthropleurids found at Mazon Creek are interpreted as fully terrestrial forms. Despite claims to the contrary, no Pennsylvanian myriapod is known to have been amphibious. The Mazon Creek forms are typically found in the Braidwood (freshwater) fauna, but some forms are also found in the Essex (marine) fauna. The presence of myriapods in a marine environment can be explained by the deltaic mode of deposition of the deposits (Baird et al., 1985) and possibly also by the presence of myriapods within coprolitic concretions (Fisher, 1979, p. 436, fig. 4f) that may have been produced by amphibious or aquatic predators moving from freshwater to saltwater habitats. Predators of myriapods who would have been capable of producing large coprolites include amphibians, reptiles, and fish. (Fish would have eaten myriapods that had fallen into the water.)

Mazon Creek myriapods are sometimes found preserved in shale matrix but are most often found preserved in concretions. These myriapods are preserved in several modes within concretions: some with their bodies outstretched, others loosely coiled (Figure 13.4).

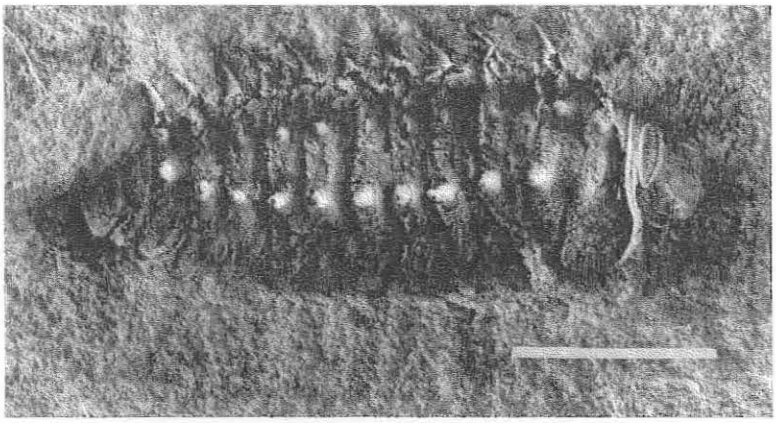

Figure 13.1. *Amynilyspes wortheni* Scudder, 1882, FMNH PE 12808; view of top and right side. The head is to the right, just beyond the small first tergite (collum). Latex cast of natural mold, from Hannibal (1984). Scale bar = 10 mm.

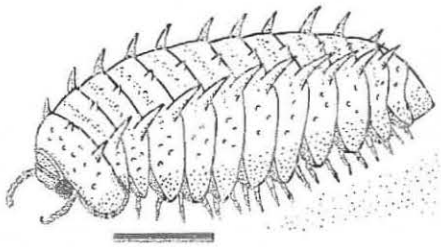

Figure 13.2. *Amynilyspes wortheni* Scudder, 1882, reconstruction based on Mazon Creek specimens, adapted from Hannibal (1984). Scale bar = 10 mm.

Coiling is a common defensive position but is also used to prevent desiccation. Complete specimens, especially of small and medium-sized forms, are sometimes found, but more often only partial specimens, especially of large forms, are found. Often body parts, such as heads and portions of the trunk, are detached. While this may be the result of natural decay before fossilization, it may also be the result of predation. Some modern predators of millipedes leave headless carcasses and disarticulated corpses behind. Some partial fossils may also represent molted cuticles.

Myriapods are typically found preserved alone but are also found preserved with plants, for instance *Pecopteris*, and occasionally with other animals, including tube worms and horseshoe crabs (Dawson, 1882; Fisher, 1979, fig. 4f).

Because many described genera and species are imperfectly known, only the well-established taxa of Mazon Creek myriapods are discussed below.

Class Diplopoda

Several types of millipedes occur at Mazon Creek. These include euphoberiids, large, long, many-segmented forms with prominent spines; the oniscomorphs, pill millipedes, so-called because of their ability to coil into a ball; and xyloiulids, more typical, garden variety millipedes, elongate, cylindrical, and many segmented. Millipedes, in part due to well-mineralized exoskeletons, are the most common myriapods found in the Mazon Creek deposits.

Most of these forms, like modern millipedes, were probably primarily detritivorous or saprophagous, ingesting decaying matter. Millipedes today are important producers of soil humus (Blower, 1985, p. 33), and this was probably the case during the Carboniferous. Burke (1979, p. 19) suggested that some forms, such as *Acantherpestes*, may have been carnivorous. There is no good evidence for such carnivory, however. While modernlike millipedes of presumably cryptic habitats are present in the Mazon Creek fauna, many Carboniferous millipedes (including euphoberiids and pill millipedes) had large eyes and spines, indicating that they lived in more open, surficial habitats (Kraus, 1974).

Superorder Oniscomorpha

Oniscomorphs (pill millipedes) have 12 to 14 body segments, a very small first tergite (collum), and a very large second tergite ("shield"). They have the ability to coil into a ball so tightly that, when enrolled, they are even watertight. Pleurites are found on the ventral side of the animal, on the outside of the legs.

Amynilyspes wortheni Scudder
Figures 13.1, 13.2

Amynilyspes wortheni is a medium-sized, spiny pill millipede with 14 tergites (one more than any modern pill millipede) and large eyes.

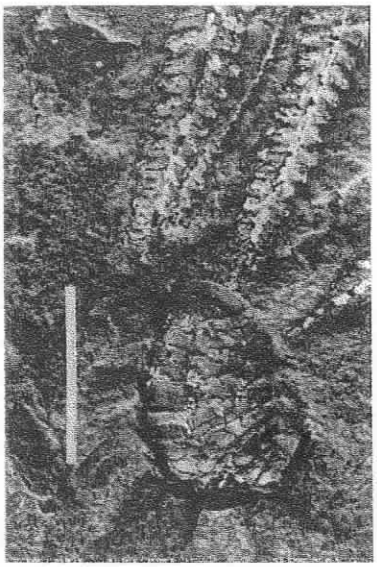

Figure 13.3. Nonspinose pill millipede, FMNH PE 29386; top view of specimen preserved in a concretion along with a front view of *Pecopteris* cf. *P. arborescens*. The exposed part of this millipede is about 13 mm (0.5 in.) long (from Hannibal, 1984). Scale bar = 10 mm.

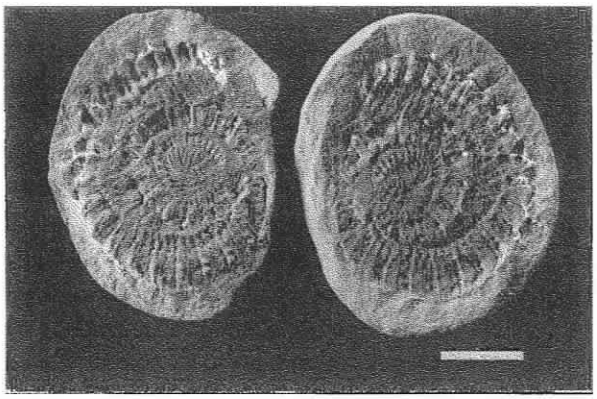

Figure 13.4. Euphoberiid millipede, FMNH PE 32243; part and counterpart. This millipede is coiled into a loose ball. The concretion is about 30 mm wide (from Hannibal, 1981). Scale bar = 10 mm. Reprinted courtesy Cleveland Museum of Natural History.

This animal was armored by large spines along the edge of its back and by a row of small spines down the middle of its back.

Most modern oniscomorphs are associated with the forest floor. Based on the presence of stout spines on this species, however, it may have lived in more open habitats, possibly including arboreal habitats (Hannibal and Feldmann, 1981, p. 744). *Amynilyspes* is the most common oniscomorph found in the Mazon Creek fauna. The type specimen of *A. wortheni* was presumably found along Mazon Creek; specimens have since been found in Pit 11 and Pits 1 and 6—thus, in both the Essex and Braidwood faunas.

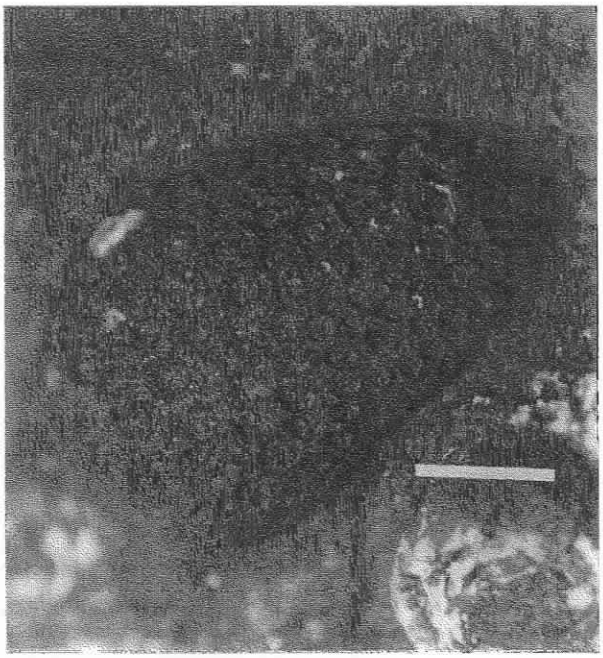

Figure 13.5. Close-up of eye of euphoberiid. The individual parts making up the aggregate eye can be seen. Scale bar = 1 mm. Photograph Bruce Frumker, Cleveland Museum of Natural History. Photograph copyright Cleveland Museum of Natural History.

Nonspinose oniscomorph
Figure 13.3

This oniscomorph, with smooth segments, originally was described (Hannibal and Feldmann, 1981) as having 13(?) tergites. Like most Carboniferous oniscomorphs, however, this form may have had 14 tergites (Hannibal, 1984). Specimens are found partly coiled. This form has been found in pits in Will and Grundy Counties, in the Braidwood fauna.

Modern forms of nonspinose pill millipedes, most of which have smooth tergites, are chiefly cryptic, adapted to burrowing and digging, but are also known to occasionally climb trees. A more cryptic, burrowing habit may explain why nonspinose oniscomorphs are less common than *Amynilyspes*. Forms living in more open habitats may be more easily washed into areas that are conducive to preservation.

Subclass Helminthomorpha

These are slender, elongate forms, with many segments. Helminthomorphs are what one thinks of as "typical" millipedes. There is

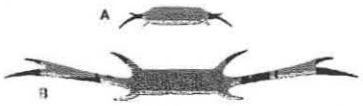

Figure 13.6. Diagram showing top view of the metazonites (posterior portions of the pleurotergites) of two of the euphoberiid genera reported from Mazon Creek: A *Euphoberia;* B *Myriacantherpestes.*

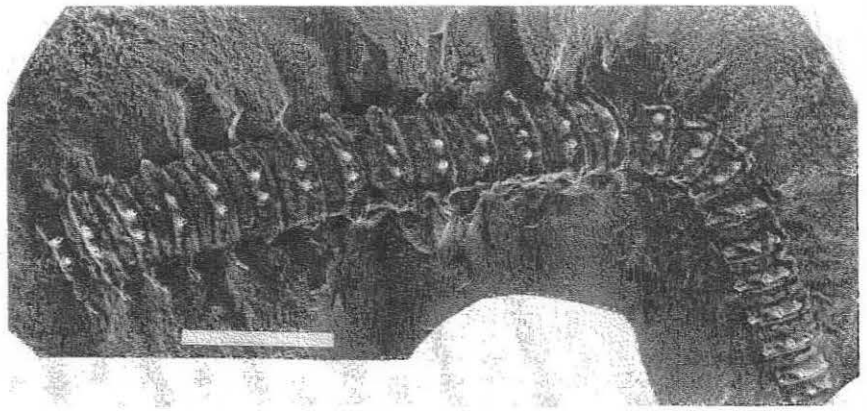

Figure 13.7. *Euphoberia carri* Scudder, 1882, USNM 38031a, in dorsal view. Specimen, including spines, is about 60 mm (about 2.3 in.) long. Note the large modified legs located on the ninth preserved body segment. Photograph is of a latex cast of a natural mold. Scale bar = 10 mm. Photograph Bruce Frumker, Cleveland Museum of Natural History. Photograph copyright Cleveland Museum of Natural History.

much variability in the configuration of the trunk segments of forms considered to be in this very large group. Some forms have clearly demarcated tergites, pleurites, and sternites; in other forms these segments are coalesced.

Order Euphoberiida
Figures 13.4–13.12

The euphoberiids (millipedes in the order Euphoberiida) are long, spinose millipedes with large heads, large aggregate eyes, and long legs. They have more than 20 and fewer than 60 body segments, ranging in length to about 300 mm (12 in.), although most forms are shorter. Each body segment is composed of two fused pleurotergal elements (coalesced coverings of the top and sides), of which the anterior is termed the prozonite and the posterior the metazonite, and has a pair of wide sternites (bottom plates). Most pleurotergites have a pair of lateral spines as well as additional, smaller spines and spinelets. The sternites have a pair of subrounded medial pores (ventral sac pits) as well as two slitlike spiracles (breathing pores), one located to the outside of each of the leg bases (coxae). Some (presumably male) specimens of euphoberiids have a pair of large modified legs (clasping appendages?) located along the midbody (Hannibal, 1995).

Euphoberiids are among the most common millipedes found at Mazon Creek, attesting to their prominence in the forests near or on the Mazonian Delta. These millipedes were probably adapted to cursorial activity in more open habitats (see Rolfe, 1985).

A number of species of euphoberiids were described from the Mazon Creek deposits by Scudder and Meek and Worthen, but not all are valid. More recent work on euphoberiids by Burke (1973, 1979) corrected a number of errors in interpretation made by these earlier workers, proving that these forms were true millipedes.

Euphoberiids typically occur in the Braidwood fauna. The relationship of this group to other helminthomorphs is unresolved.

Genus *Euphoberia*
Figures 13.6A, 13.7

The genus *Euphoberia* includes small to medium-sized euphoberiids, typically 80–150 mm (3–6 in.) in length. Metazonites of these millipedes have relatively short lateral spines, lacking the small anterior spines in front of these spines that are present in the genus *Myriacantherpestes.* Also, there are a pair of spines near the middle of the back (paramedian spines), each with an anterior spinelet. A large number of species of *Euphoberia,* not all of them valid, have been described. Meek and Worthen (1868, p. 26) described the origin of this generic name, which at first included the genera now known as *Euphoberia* and *Acantherpestes,* as follows: "For this uncouth looking creature, we would propose the generic name *Euphoberia* ["spiny creeper"], in allusion to the formidable appearance a living example, more than a

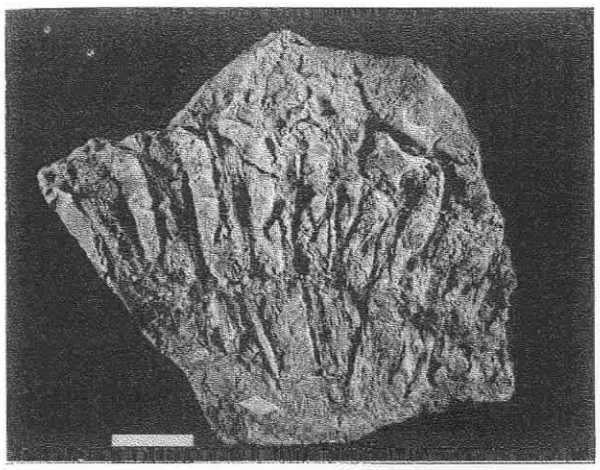

Figure 13.8. *Acantherpestes major* (Meek and Worthen), holotype, UI X504, mostly in top view. Specimen is about 60 mm (about 2.3 in.) long. Most of the spines of this specimen have been broken off; several legs can be seen extending from the bottom of the specimen (from Burke, 1973, fig. 3). Scale bar = 10 mm. Reprinted courtesy Cleveland Museum of Natural History.

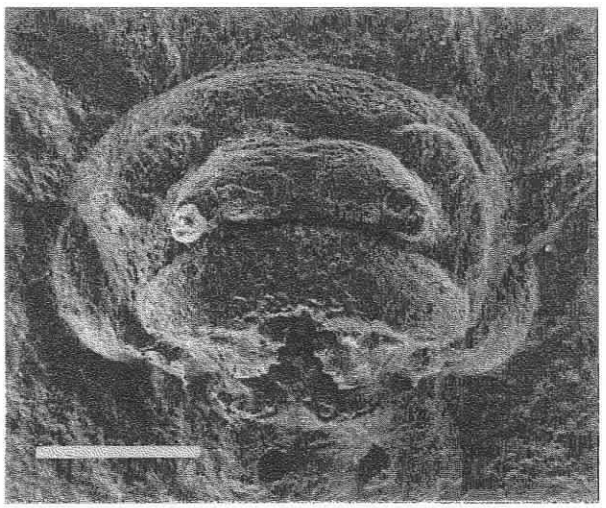

Figure 13.9. *Myriacantherpestes*?, Wallis Triebull collection. The eyes, antennal bases, and mandibles can be seen. Scale bar = 5 mm. Photograph Bruce Frumker, Cleveland Museum of Natural History. Photograph copyright Cleveland Museum of Natural History.

foot in length, must have presented, when alive and moving about, with its back bristling with forked spines, and its 150 legs in motion."

Genus *Acantherpestes*
Figure 13.8

This large euphoberiid ranges in size to about 300 mm (12 in.). It bears lateral spines, lacking small anterior spines, and has simple paramedian spines. The holotype of *Acantherpestes major* (Meek and Worthen) has been restudied by Burke (1973) and is illustrated here as Figure 13.8. Many of the well-known specimens of *A. major* were removed from the genus *Acantherpestes* by the actions of Burke (1979) when he erected the new genus *Myriacantherpestes*.

Burke (1973, p. 22) hypothesized that "protected from most predators by sheer size, *Acantherpestes* was probably able to move about freely" and that it may have "ventured into open areas of the lowlands bordering the Carboniferous swamps." He also suggested that this form may have been carnivorous.

Genus *Myriacantherpestes*
Figures 13.6B, 13.9–13.12

This medium-sized to large euphoberiid has very long lateral spines, anterior spines, and simple paramedian spines or nodes. It can be distinguished from *Euphoberia* and *Acantherpestes* by the presence of anterior spines (Burke, 1979, p. 16). One of the largest species of this genus is *Myriacantherpestes hystricosus* (Scudder), which may have reached 300 mm (12 in.) in length.

Burke (1979) found this form to be adapted to a "bulldozer" function, akin to that of some modern millipedes that push through the leaf litter of forests. This is unlikely, however, as the large spines of the animal would have made this practically impossible (W. Shear, personal communication, 1992). It probably lived in more open habitats.

Order Spirobolida
Family Xyloiulidae

These are Paleozoic millipedes with cylindrical body segments composed of mostly coalesced pleurites, tergites, and sternites. The pleurotergites are covered, or mostly marked, with a series of horizontal or oblique ridges and grooves (Hoffman, 1969, p. R587). Similarly shaped modern millipedes are sometimes known as "snake millipedes."

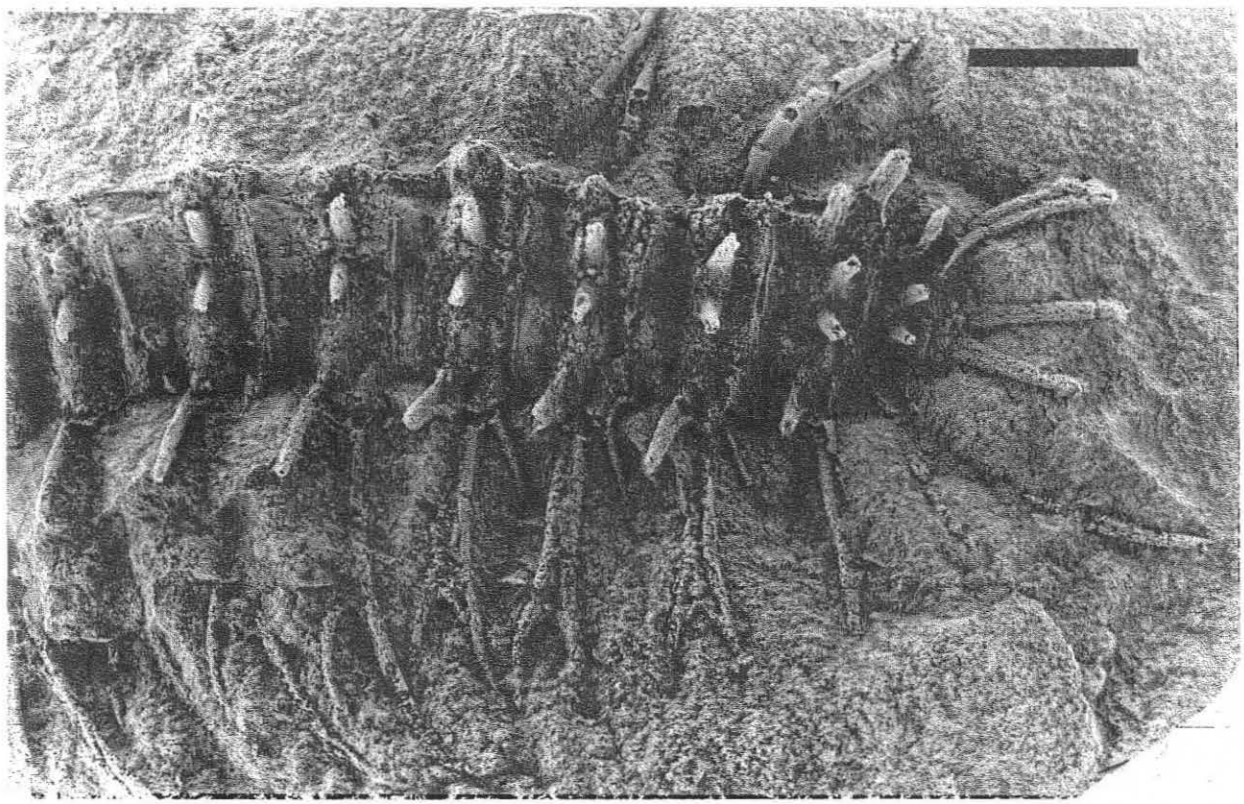

Figure 13.10. *Myriacantherpestes hystricosus* (Scudder), CMNH 3725 (coll. Wilbert A. Rath); top view of posterior of the millipede. This form has especially long, elegant lateral spines. The smaller spines, just to the anterior and posterior of the large lateral spines, that characterize this species can be seen along the left side of the animal. Three legs can be seen along the right side. Spines included, this millipede was about 65 mm (2.5 in.) wide in life. Photograph of a latex cast of a natural mold (from Hannibal, 1986). Scale bar = 10 mm. Reprinted permission *Earth Science* magazine, published by the American Geological Institute.

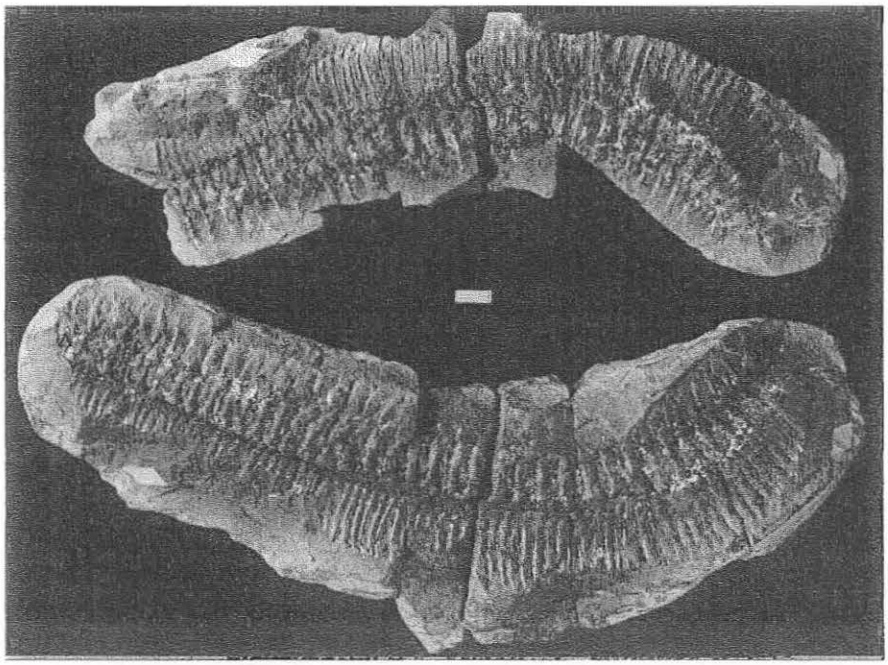

Figure 13.11. *Myriacantherpestes hystricosus* (Scudder), USNM 38038. This large specimen, about 200 mm long, is enclosed in a 220 mm (about 9 in.) long concretion. It was originally classified as *Acantherpestes major* by Scudder (1882), who called it "the most perfect large specimen that has been discovered." It has been one of the most commonly illustrated specimens of euphoberiid millipede, often referred to as "giant spined myriapods." From Hannibal, 1986. Scale bar = 10 mm. Reprinted permission *Earth Science* magazine, published by the American Geological Institute.

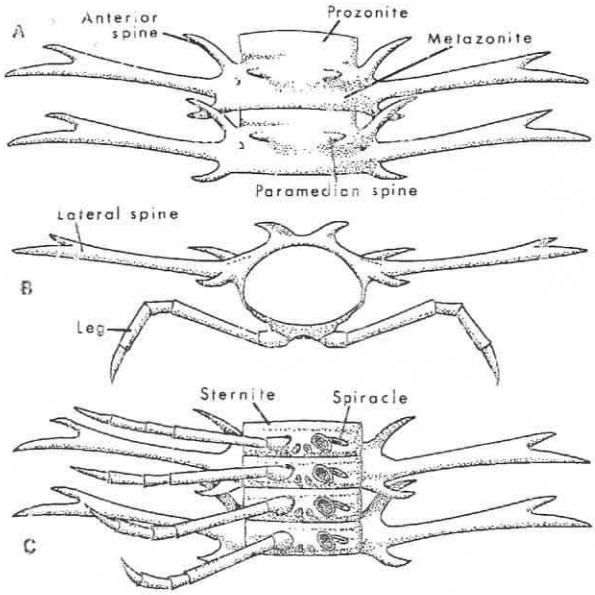

Figure 13.12. Drawing showing a typical midbody segment of a generalized *Myriacantherpestes* in top (*A*), cross-sectional (*B*), and bottom (*C*) views. *A* and *C* adapted from a drawing by Brant Gebhart, Cleveland Museum of Natural History; *B* adapted from Burke (1979, fig. 1). The interpretation of the morphology shown in these drawings is based on the work of Burke (1973, 1979).

Genus *Xyloiulus*

This form is elongate and has more than 50 segments. Horizontal ridges and grooves mark the pleurotergites.

Like most modern long, elongate millipedes, this millipede was probably cryptic, burrowing into the leaf litter and upper layers of the soil. Xyloiulids are typically found in the Braidwood fauna. A photograph of a loosely coiled specimen can be found in Baird et al. (1985, fig. 5.3).

Class Chilopoda

Centipedes are quick-moving, carnivorous myriapods with from 15 to 181 pairs of legs, one pair per segment. Their bodies are flattened from top to bottom, and they have large pincer-like claws through which they inject poison into their prey (small insects, insect larvae, and other small invertebrates). Centipedes live in a wide variety of habitats, typically in the leaf litter of the forest and in the upper layers of the soil, but some forms are even known to live in the intertidal zone along the seashore (Lewis, 1981, pp. 384–385). They have relatively soft

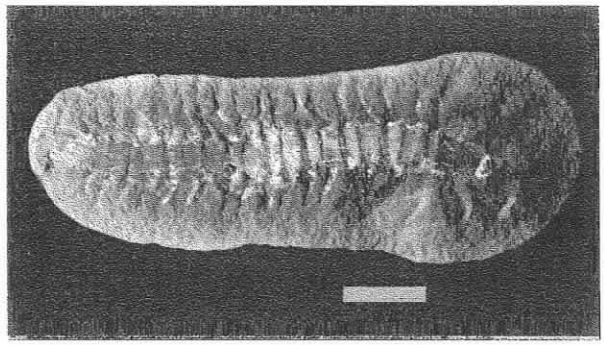

Figure 13.13. *Mazoscolopendra*. Most of the legs and body segments of this centipede can be seen in this view. Scale bar = 10 mm (estimate).

and unmineralized exoskeletons and are not nearly as common as fossils as are millipedes. At least three genera of centipedes, however, have been found at Mazon Creek.

Order Scolopendromorpha

Scolopendromorph centipedes are small to large centipedes with 21 to 27 trunk segments, 21 or 23 pairs of long legs, and antennae with up to 30 segments. The largest modern centipedes belong to this group. Modern scolopendrids live in a variety of habitats including the leaf litter and upper layers of the soil (Hoffman, 1982, p. 683). They are known to eat a wide variety of prey, including worms, nymphal cockroaches, flying insects, mites, spiders, toads, snakes, and mice (Lewis, 1981, pp. 172–174).

Mazoscolopendra richardsoni Mundel
Figure 13.13

This centipede, up to 53 mm (2 in.) long has 21 leg-bearing trunk segments, long legs, and antennae with at least 14 segments (Mundel, 1979, pp. 363–366). Its name, loosely translated, is "Richardson's Mazonian centipede." The second most common centipede at Mazon Creek, *M. richardsoni* has been reported from Pit 11, an Essex fauna locality.

Palenarthrus impressus Scudder

Palenarthrus impressus is characterized by flattened rectangular tergites. It was originally described by Scudder (1890) based on a 46 mm (almost 2 in.) long specimen with about 23

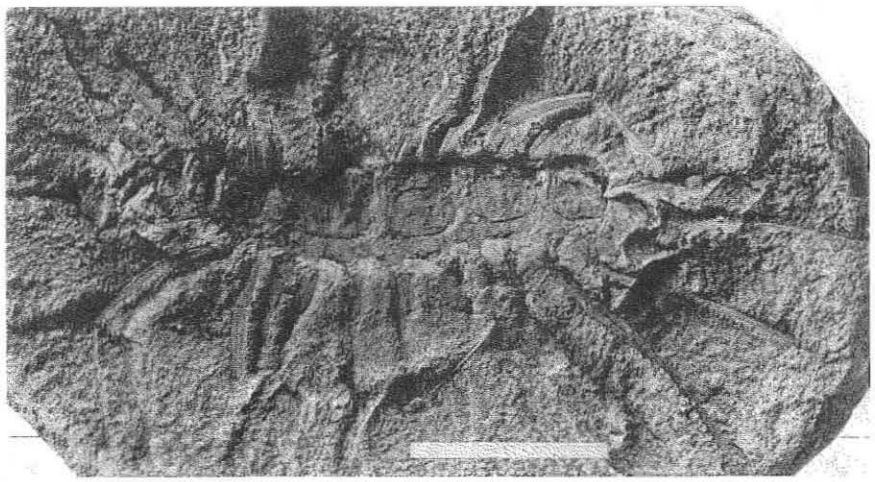

Figure 13.14. *Latzelia primordialis* Scudder, CMNH 8672. Most of the tergites (rectangular plates covering the back) and many of the long legs of this centipede can be seen in this view. This specimen is almost 30 mm (about 1.2 in.) long. Scale bar = 10 mm. Photograph copyright Cleveland Museum of Natural History.

preserved segments and long legs. Mundel (1981) reaffirmed its identity as a scolopendromorph, noting that Scudder had originally described the rear of the animal as the front! It is found among the Braidwood fauna.

Order Scutigeromorpha

Scutigeromorph centipedes are swift-moving predators, with very long antennae and 15 pairs of very long legs. They dwell along the surface of the forest and are excellent climbers. They have spiracles (breathing pores) located along the back edge of the top of the tergites. The common house centipede of North America, *Scutigera coleoptrata* (often observed while stalking prey on ceilings or scurrying across floors), is a member of this group.

Scutigeromorphs are known to consume a variety of prey, including house flies, moths, spiders, worms, cockroaches, and sow bugs (Lewis, 1981, pp. 183–186).

Latzelia primordialis Scudder
Figure 13.14

This species had seven smooth, gently arched tergites; a moderately sized head; and very long legs. It has been redescribed by Mundel (1979, pp. 366–373), who has shown this form to be quite similar in general aspect to, but larger and more robust than, *Scutigera coleoptrata*. Like its modern relatives it was a swift-moving predator. Its generic name is in honor of Robert Latzel, a nineteenth-century Viennese myriapod worker. The original specimen was presumably collected along Mazon Creek. The collection at the Field Museum of Natural History examined by Mundel (1979) contained specimens from Pit 11, from the Essex fauna. This is the most common centipede found at Mazon Creek (Mundel, 1981).

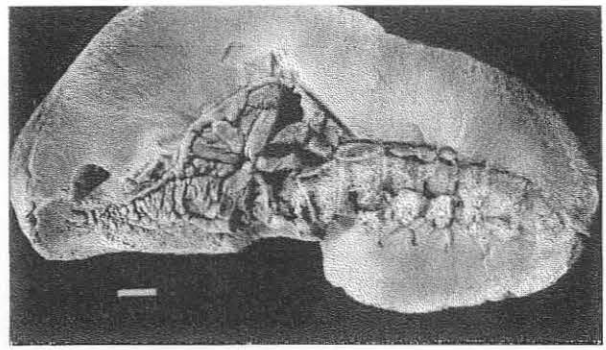

Figure 13.15. *Arthropleura cristata* Richardson, USNM 439582 (coll. Mrs. John McLuckie). Left leg of a medium-sized specimen. Scale bar = 10 mm.

Class Arthropleuridea
Order Arthropleurida
Figures 13.15–13.17

These extinct, many-legged, animals are among the very largest known terrestrial arthropods. They ranged in size up to 2 m and were possibly even longer. Arthropleurids had about 30 spinose, tuberculate tergites divided into three lobes by longitudinal grooves (a superficial resemblance to trilobites that resulted in their once being classified in the Trilobitomorpha). Each trunk segment bore two pairs of legs, at

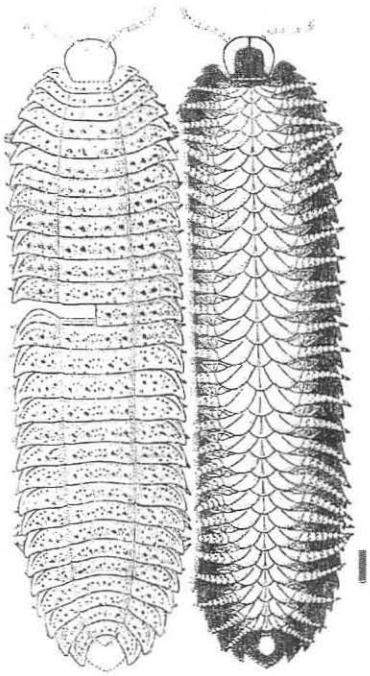

Figure 13.16. *Arthropleura armata* Jordan and Meyer; reconstruction, top (*left*) and bottom (*right*) views. Half of one tergite removed to show anterior border of underlying tergite; no limbs are shown on first trunk somite. Interrupted lines indicate restored regions of body. Study of complete specimens by Hahn et al. (1986) shows that the animal tapered more toward the front and the rear than shown here. It also appears likely that (Almond *in* Briggs et al., 1984) *Arthropleura* possessed more than one pair of limbs per segment, on average. Some individuals grew to more than 1 m in length. Illustration by J. K. Ingham from W. D. I. Rolfe and J. K. Ingham (1967, fig. 2). Scale bar = 100 mm (estimate). Reprinted from the Scottish Journal of Geology; courtesy Scottish Academic Press (Journals) Limited.

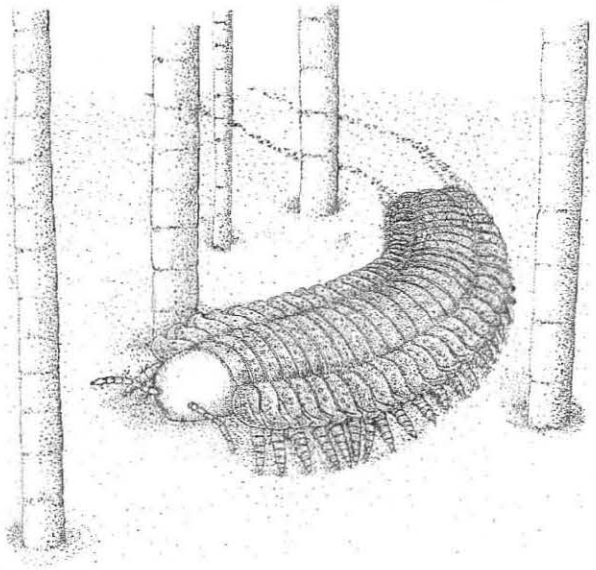

Figure 13.17. Reconstruction of 2 m long *Arthropleura* moving through a Carboniferous forest. Drawing by Annemarie Burzynski from Briggs, Plint, and Pickerill (1984, text-fig. 5). Reproduced courtesy Palaeontological Society.

least on some segments (Almond *in* Briggs et al., 1984; Briggs and Almond, 1994). Large rosette plates (convex, irregularly oblong plates divided into several lobes, bearing a resemblance to flower petals) are found near the base of the legs.

Fossils of whole or partial skeletons of arthropleurids, as well as large trackways made by them, are known from a number of localities in North America and Europe (Briggs et al., 1984). Only partial specimens, consisting of portions of legs, rosette plates, and portions of tergites, have been described from Mazon Creek.

Arthropleura cristata Richardson
Figure 13.15

Richardson (1956) was the first to accurately describe specimens of *Arthropleura* from Mazon Creek. Later (1959), he named a new species, *A. cristata*, designating a specimen consisting of the dorsal surface of a single paratergal fold (lateral part of a tergite) as the holotype. This very large species is characterized by a row of large spines near the back border of the paratergal fold accompanied by a row of smaller spines even nearer to the border, and other characters. This rare form is found within the Braidwood fauna. Although there have been a number of good papers (e.g., Rolfe, 1969; Hahn et al., 1986) on arthropleurids, there has been little subsequent work on the classification of arthropleurids from Mazon Creek since Richardson's work. Most specimens from Mazon Creek consist of isolated limb fragments and rosette plates.

The flattened body form of *Arthropleura* and the layers of lycopod tree debris sometimes found fossilized in its guts suggest a life in the surface layers of litter along the forest floor, burrowing within the rotting trunks of lycopod trees (Rolfe, 1980, 1985). However, trace fossils made by these large beasts indicate that they could roam about sandy areas as well (Rolfe, 1985; Briggs et al., 1984).

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